Thema

The Role of the Medial Prefrontal Cortex in Mediating Social Event Knowledge

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1. Introduction

Social event knowledge is abstraction-derived from concrete experience of social life — its content originates in human interaction and constructs the understanding of the social world. The social brain hypothesis links evolutionary pressure for brain enlargement and specialization to the need of solving problems in socially complex environments (Dunbar, 1998). This hypothesis (put forward originally by Jolly (1966) and Humphrey (1976)), and ultimately in fully fledged form as the "Machiavellian intelligence hypothesis" by Bryne and Whiten (1988) argues that the complex nature of our ancestors sociality, involving both the formation of intense social relationships and the use of coalitions in cooperative defense, imposed unusually heavy demands on their capacities to make inferences about the future behavior of other group members. The sophisticated neural architecture of the human prefrontal cortex (PFC) along with the sustained firing of its neurons (Fuster and Alexander, 1971) and the ability to integrate a larger amount of excitatory inputs from many sources (Elston, 2000) provided a vehicle for the emergence of social cognition (Adolphs, 2003).

If brain size is driven by the demands of sociality, what kind of cognitive mechanisms can bridge the gap between brain and social behavior? The social brain is an organ of adaptation that builds its structure through interactions with others. Studies of functional specialization within the PFC have emphasized the distinction between lateral and medial PFC areas (Elliott et al., 2000; Gilbert et al., 2006a; Gilbert et al., 2006b). Because the medial PFC (mPFC) is phylogenetically and ontogenetically older than the lateral PFC, a functional dissociation evolved in which the mPFC became capable of encoding stable, internally focused, mental-oriented representations compared to adaptive, externally focused, control-oriented representations encoded in the lateral PFC (Barbey et al., 2009; Koechlin et al., 2000; Krueger et al., 2009a; Lieberman, 2007; Wood et al., 2005).

The representation of social event knowledge provided humans with an instrument for interpreting and acting on a social reality that would otherwise be unpredictable. Over the course of evolution, precursors of social event knowledge began to serve specific goals to improve social interaction and intelligence by providing interpretive context for agents, actions, objects, and settings to be found in the social world. As a consequence, specialized neural systems in the mPFC emerged that enabled the encoding of social event knowledge that is intimately involved in both planning and

monitoring one's own behavior as well as understanding and predicting the behavior of others.

Most current theories of PFC function focus on lateral PFC subregions (Badre, 2008; Botvinick, 2008; Christoff and Gabrieli, 2000; Duncan, 2001; Fuster, 2001; Koechlin and Summerfield, 2007; Miller and Cohen, 2001; Ramnani and Owen, 2004), whereas a systematic analysis of mPFC subregions in the context of social functions only began recently (Amodio and Frith, 2006; Van Overwalle, 2008). Although nonhuman primate research has not been particularly helpful in identifying higher-order social mPFC functions, however, accumulating evidence from functional neuroimaging studies in humans has demonstrated that besides the temporal pole, superior temporal sulcus, temporoparietal junction, and amygdala (Frith and Frith, 2006), subregions of the mPFC are also core regions of social cognition (Amodio and Frith, 2006; Van Overwalle, 2008). Even though it is acknowledged that the mPFC mediates social event knowledge (Heberlein, 2008; Krueger and Grafman, 2008; Krueger et al., 2007b; Wood et al., 2005), the underlying neural structures of social event knowledge and the nature of its functional subdivisions within the mPFC are still obscure.

Some current cognitive neuroscience frameworks have direct implications for the understanding of the neural basis of social event knowledge, but each has its own limitations with respect to their relevance for social event knowledge (Damasio, 1996; Grafman, 1995; Moll et al., 2005). For example, although the somatic marker hypothesis has been influential and is considered to be a possible mechanism that could underlie the emergence of social event knowledge (Damasio, 1996), this framework does not explicitly address the role of different PFC subregions in mediating social event knowledge. Furthermore, the structured event complex framework supports claims that executive functions performed by the PFC are based on stored event sequence knowledge that have clear implications for social event knowledge (Grafman, 1995), but it does not predict how PFC regions interact with limbic areas and other cortical regions to give rise to a wide variety of social cognitive functions leading to goal-directed social behaviors. Finally, the event-feature-emotion complex framework explains how cultural and context-dependent knowledge, semantic social knowledge and motivational states can be integrated to explain complex aspects of moral cognition (Moll et al., 2005). However, moral cognition only accounts for some aspects of social event knowledge which is of vital importance for the emergence of traits represented in person and self schemata.

In this synopsis, I sketch out an *integrative theory* —entitled *S*tructural and *T*emporal *R*epresentation Bind*ing* (STRing) theory— of the neural and cognitive basis of social event knowledge (Krueger et al., 2009a). I draw together the elements of the theory from four principal components: evolution, neuroanatomy, cognition, and behavior. This theory will necessarily be incomplete, but I hope to show that by drawing these components together into a single coherent framework, one might gain further knowledge of the underlying cognitive and neural representations involved in social event knowledge. First, I summarize the key elements of the evolution and biology of the human PFC. I argue that the STRing theory is consistent with what is known about the evolution, structure, connectivity, development, and neurophysiology of the PFC. Second, I describe the principles of the STRing theory. I argue that the mPFC represents *e*vent simu*lators* (elators) that give rise to social event knowledge via structural and temporal representation binding with regions in the posterior cerebral cortex and subcortical brain structures. Finally, I review the different lines of evidence to support the STRing theory by focusing on neuroimaging studies. I argue that components of social event knowledge are of vital importance for the simulation of event schemata, person schemata, and self schemata that serve a wide variety of social cognitive functions leading to goal-directed social behaviors.

1.1 Evolution and Biology of the Human Prefrontal Cortex

Over millions of years, natural selection slowly shaped the human brain favoring neural circuits that were good at solving adaption problems of our ancestors. As the result, brains evolved and grew from back (the visual areas) to front (the so-called executive brain) creating brains with more complex abilities. Importantly, increases in brain volume across primates were driven largely by a disproportionate increase in frontal lobe volume that lead to evolutionary advances from primates to humans (Chiavaras et al., 2001; Elston, 2000; Elston and Rosa, 2000) emerging to a more sophisticated internal and differentially organized neural PFC architecture (Chiavaras et al., 2001; Elston, 2000; Elston and Rosa, 2000). For example, the human PFC (the frontal pole, Brodmann's area 10, in particular) is proportionally larger to the rest of the cerebral cortex compared to the PFC of primates (Rilling and Insel, 1999; Semendeferi et al., 2001; Semendeferi et al., 2002). Furthermore, neurons in the human PFC have the ability to sustain their firing and code the temporal and sequential properties of ongoing events

in the environment over longer periods of time (Levy and Goldman-Rakic, 2000; Rueckert and Grafman, 1998). Moreover, pyramidal cells in the human PFC are significantly more spinous compared to other cortical areas, making them capable of handling a larger amount of excitatory inputs (Elston, 2000; Elston and Rosa, 2000). Finally, following general patterns of brain ontogeny (neurogenesis, early, dense synapse formation followed by synaptic pruning and myelination), the PFC undergoes relatively late postnatal development compared to other cortical association areas (Conel, 1939; Flechsig, 1920; Huttenlocher, 1990; Huttenlocher and Dabholkar, 1997). It does not fully mature until adolescence and early adulthood leaving a great deal of neural plasticity to adjust to circumstances in the environment (Chugani et al., 1987; Diamond, 1991; Durston et al., 2001; Giedd et al., 1999; Paus et al., 1999; Sowell et al., 1999). Although many social cognitive abilities in humans first emerge during the period of peak synaptic density, many of our more complex social cognitive functions do not reach adult level of efficiency and competence until late adolescence or early adulthood, after the most pronounced phases of synaptic pruning have been completed (Blakemore, 2008).

The human PFC occupies approximately one-third of the entire human cerebral cortex and has a columnar design like other cortical regions. Some regions of the human PFC have a total of 6 layers; other regions are agranular (without a granular cell layer). It can be subdivided into lateral, medial, and orbitofrontal regions (Fig. 1), in which Brodmann's areas (BA, 8-11, 23-25, 32, 44-47) provide the cytoarchitectonic subdivision within each of these gross regions (Barbas, 2000; Brodmann, 1912; Stuss and Benson, 1986). In particular, the mPFC –consisting of medial orbital frontal cortex (mOFC), ventral mPFC (vmPFC), and dorsal mPFC (dmPFC)– has considerably increased in size in recent evolution in the brains of primates. Importantly, medial and lateral human PFC belong to two distinct cytoarchitectonic trends within the human PFC (Pandya and Yeterian, 1996). The medial trend is phylogenetically and ontogenetically older than the lateral trend, which is especially well developed in humans (Stuss and Benson, 1986). The PFC subregions are interconnected with other areas of the brain and almost all of these pathways are reciprocal (Alexander et al., 1990; Masterman and Cummings, 1997). In particular, the mPFC has strong limbic system connections via its medial and orbital efferent connections that terminate in the amygdala, thalamus, and parahippocompal regions (Groenewegen and Uylings, 2000; Price, 1999) and long pathway connections to association cortices in the temporal, parietal, and occipital lobes.

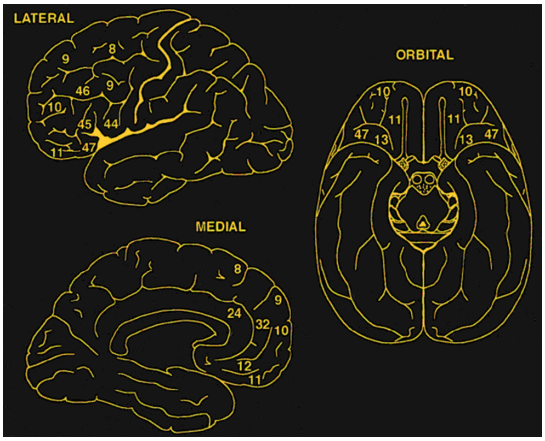

Figure 1. Structure of the human prefrontal cortex. Adapted from Fuster (2001).

In summary, the evolution and the biology of the human PFC are strongly suggestive of its role in the integration of sensory and memory information as well as in the representation and control of actions and behavior. Along with extended firing of neurons, specialized neural systems were developed that enabled the encoding of these social behaviors into sequentially linked, individually recognizable events. The event sequence itself must be parsed as each event begins, and ends, in order to explicitly recognize the nature, duration, and number of events that compose this sequence (Zacks et al., 2001; Zacks and Tversky, 2001). These event sequences, to be goal-oriented and cohere, must obey a structure that can be conceptualized as a representation (i.e., a 'permanent' unit of memory that), when activated, corresponds to a dynamic brain state signified by the strength and pattern of neural activity in a local PFC sector. In this sense, over the course of evolution, specialized neural systems in the mPFC emerged hat enabled the encoding and retrieval of social event knowledge into abstract dynamic structured summary representations that can be used to guide social self- and other-related goal-directed behavior over a longer period of time (Barbey et al., 2009; Huey et al., 2006; Rueckert and Grafman, 1998; Wood and Grafman, 2003).

1.2 Principles and Predictions of the STRing Theory

Because the design of the brain owes its functional organization to a natural, evolutionary process, an evolutionarily cognitive neuroscience approach for a theory of social event knowledge is a logical consequence. The STRing theory relies on the concept of abstract dynamic structured summary representations (Barsalou, 1999; Damasio, 1989), which have its roots in mechanisms that are grounded both in brain

architecture and in principles of neural processing (Barsalou, 2008b). According to this view, representations have no existence separate from processes, but are instead embedded in, distributed across, and hence, inseparable from one another (Barsalou et al., 2007). The STRing theory seeks to establish the format and domain specificity of representations according to which the same fundamental processes operate on different categories of information regarding social event knowledge.

According to the STRing theory, the mPFC represents elators that give rise to social event knowledge via structural and temporal representation binding with regions in the posterior cerebral cortex and subcortical brain structures (Fig. 2). Elators are information-processing modules that were selected throughout the human's evolutionary history, because they are economic, efficient, and reliable solutions in producing social behavior that solved particular adaptive social problems. In particular, elators capture the sequence of previously encountered social events that are semantically structured by distinctive features such as agents, actions, objects, and settings (Krueger, 2000). For example, the abstraction for 'hosting a birthday party' represents a sequence of events (e.g., the host invites guests to the birthday party, bakes a cake, lights the candles, presents the cake to the birthday boy, sings "happy birthday") that involve agents (e.g., host and birthday boy), actions (e.g., baking a cake and lighting the candles), objects (e.g., birthday cake and candles), and background settings (e.g., dining room). Importantly, elators are temporally organized on the basis of (i) *goals* that enable the selection of goal-directed event sequences, and (ii) *outcomes* that enable the selection of the affective responses and reward values associated with goal achievement.

Elators as abstract dynamic structured summary representations are learned and developed over time through direct and indirect perception and experience of social situations. Three central properties of elators exist, which together can be defined as a summary representation of a category of knowledge in long-term memory (Barsalou, 2003): (1) Elators are closely linked to *interpretation*, i.e., once a concept for social event knowledge has been abstracted from experience, its summary representation supports the subsequent interpretation for later experiences. (2) Elators are organized into *structured representations*, i.e., they get rather assembled into structured representations that interpret complex structures than interpreting isolated components of social experiences in the world. (3) Elators are *dynamic summary representations*, i.e., instead of a single abstraction representing a social event knowledge category, an infinite

number of diverse abstractions can be constructed to represent a social event knowledge category temporally.

Elators are encoded and retrieved on the basis of simulation mechanisms (Barsalou, 1999). It is now widely accepted that the human brain relies heavily on parallel processing. When a social situation is perceived or experienced, feature detectors in relevant modalities of the brain capture modality-specific states, and neurons in nearby association areas store the patterns' features to represent aspects of this experience. For example, social perceptual features (e.g., face, voice, and body posture of the agent) are captured in the anterior and posterior temporal cortex, action features (e.g., socially-centered action sequences) in the pre-motor cortex, and emotional features (e.g., happiness) in limbic structures. Association areas exist at multiple hierarchical levels ranging from posterior association areas to increasingly complex association areas in anterior brain regions (Duncan, 2001). Importantly, the mPFC —located at the apex of this hierarchy— binds simpler features from different modalities. In particular, PFC neurons conjoin patterns of these features across association areas and time, uniquely capturing the structured and temporally organized components of social event knowledge on the basis of *goals and outcomes* represented by the social situation.

As multiple instances of the same social situation are perceived or experienced, they recruit similar neural states in modality-specific feature maps and activate similar association areas. As the consequence, neurons in the PFC capture diverse exemplars of social situations, establishing an elator that encompasses an abstract dynamic multi-modal summary representation distributed throughout the brain's association and modality-specific areas. Mere observation, recognizing, or thinking of a similar situation triggers the activation of a subset of neurons in the mPFC and partially reactivates elator components in the absence of bottom-up sensory stimulation so that inferences about the situation can be drawn via pattern completion with all components simulated (Barsalou et al., 2003). The reenactment of elator content arises through structural and temporal binding by oscillatory firing patterns of neurons with frequencies in the gamma-range (Engel and Singer, 2001) of distributed representations stored in spatially separate cortical areas in the posterior cortex and subcortical structures.

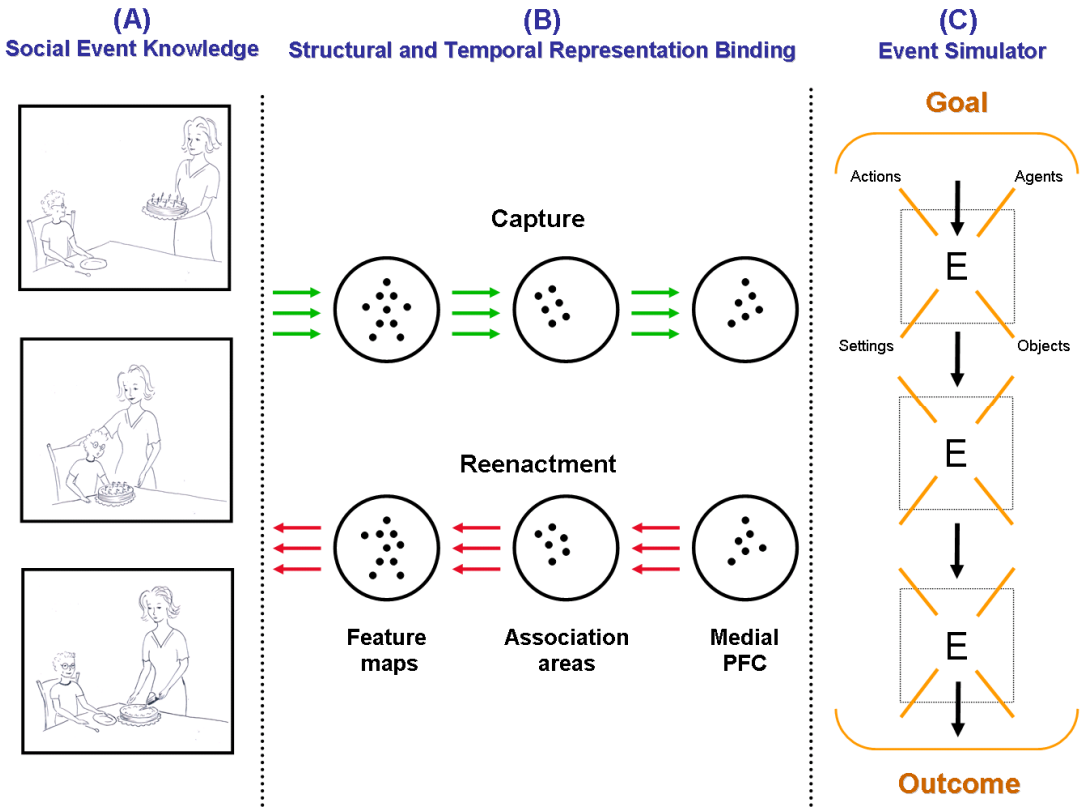

Figure 2. STRing theory. **(a) Social event knowledge**. The abstraction for 'hosting a birthday party' represents a sequence of events (e.g. the host invites guests to the birthday party, bakes a cake, lights the candles, presents the cake to the birthday boy, sings 'happy birthday') that involve agents (e.g. host and birthday boy), actions (e.g. baking a cake and lighting the candles), objects (e.g. birthday cake and candles), and background settings (e.g. dining room). **(b) Structural and temporal representation binding**. *Capture*: Feature detectors in relevant modalities of the brain capture modality-specific states, whereas nearby association areas store the patterns' features to represent aspects of experience. The mPFC conjoins patterns of activation across association areas and time, capturing the semantically structured and temporally organized components of social event knowledge into an elator. *Reenactment*: Once an elator exists, it can reenact small subsets of its content as specific elations. The reenactment of elator content arises through structural and temporal representation binding that encompasses a multi-modal representation distributed throughout the brain's association and modality-specific areas. **(c) Event simulator (elator)**. Elators are structured by events that are defined by distinctive features such as agents, actions, objects, and settings, and temporally organized on the basis of goals enabling the selection of goal-directed event sequences and event outcomes enabling the selection of the affective responses and reward values associated with goal achievement. Adapted from Krueger et al., (2009a).

According to the STRing theory, elator functions are organized along a dorso-ventral spatial gradient that maps directly onto the anatomical architecture of the mPFC (Barbas et al., 1999; Carmichael and Price, 1996; Ongur et al., 2003) (Fig. 3). The dorso-ventral gradient is characterized by a continuum between elators mediating *goal knowledge* versus elators mediating *outcome knowledge* derived from social event knowledge. On the one hand, goal knowledge supports inferences about the likely actions performed by agents for goal achievement and preferentially recruits the dmPFC.

This *goal pathway* has reciprocal connections with brain regions that are associated with motor control (premotor cortex, and supplementary motor area), performance monitoring (cingulate cortex), and higher-order sensory processing (association areas, parietal cortex) (Ongur et al., 2003). On the other hand, outcome knowledge enables inferences about likely affective responses and reward values for agents accompanying goal achievement and preferentially recruits the vmPFC/mOFC. This *outcome pathway* has reciprocal connections with brain regions that are associated with emotional processing (amygdala), memory (hippocampus), reward processing (basal ganglia including the striatum and the nucleus accumbens) and higher-order sensory processing (temporal visual association areas) (Ongur et al., 2003). Importantly, as one moves more rostrally within the mPFC, progressively more complex elators are represented, which are hierarchically organized and guide social behavior over progressively longer temporal intervals. The hierarchical structure of elators maps directly onto the anatomical hierarchical architecture of the mPFC (Badre, 2008; Botvinick, 2008; Fuster, 1997). Since the most rostral part of the PFC (Brodmann's area 10) is one of the last brain regions to mature (Giedd et al., 1999), it is ideally suited to represent more complex elators that integrate information from the goal pathway with information from the outcome pathway.

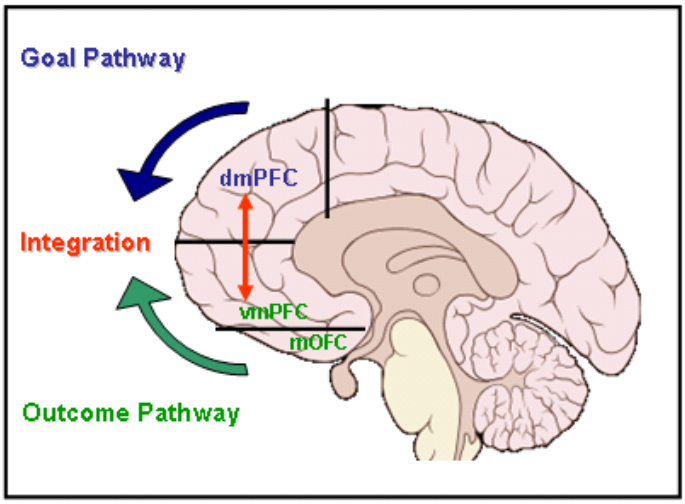

Figure 3. Elator functions and spatial gradients in the mPFC. The mPFC consists of three sectors: mOFC (z<-15mm of the Talairach atlas), vmPFC (z<20mm), and dmPFC (z≥20mm). The goal knowledge pathway in the dmPFC supports inferences about the likely actions performed by agents for goal achievement. The outcome knowledge pathway in the vmPFC/mOFC enables inferences about the likely affective responses and reward values for agents accompanying goal achievement. Most rostral parts of the mPFC mediate more complex elators that allow integration of information from the goal pathway with information from the outcome pathway. Adapted from Krueger et al., (2009a).

1.3 Neuroscience Evidence in Support of the STRing Theory

Once elators have been abstracted from experience with daily life situations, their abstract dynamic structured summary representations support the interpretation of future behaviors. Components of social event knowledge can be reenacted temporally as simulations and tailored to the constraints of the current social situation serving a wide variety of social cognitive functions. The STRing theory predicts that different components of social event knowledge are of vital importance for the simulation of *event schemata, person schemata,* and *self schemata.* Importantly, those schemata are both overlapping and distinct cognitive concepts (Fiske and Taylor, 1991; Taylor and Crocker, 1981) allowing to integrate information over time into a more general and abstract notion of social conduct such as categorizing social entities and events, drawing social inferences, and planning and remembering social interactions (Barresi and Moore, 1996; Barsalou, 2008a). They can be seen as *shared representations* that have the capacity to coordinate first-person and third-person information via a single conceptual system. Therefore, the interaction of these schemata allows for a direct, experiential first-person understanding of third-person behavior (Decety and Sommerville, 2003). Understanding our own behavior allows us to relate to and understand the behavior of others, which opens up possibilities for more sophisticated social behavior.

Event Schemata. Event schemata describe the sequential and hierarchical organization of events derived from everyday activities (Nelson and Gruendel, 1981; Schank and Abelson, 1977). The STRing theory predicts that the *sequential knowledge* component of social event knowledge is of crucial importance for event schemata: elators represented in the mPFC simulate event schemata that organize and guide the sequential and hierarchical organization of events in daily life activities. To test this hypothesis, three functional magnetic resonance imaging (fMRI) experiments were performed to investigate the underlying neural structure of event schemata by *focusing on the sequential knowledge component of social event knowledge*:

Experiment 1. The first fMRI study investigated the patterns of brain responses when participants were engaged in judgments about the sequential organization of low frequency (e.g., going to a funeral), moderate frequency (e.g., going bowling), and high frequency (e.g., going out for dinner) daily life activities based on normative data

(Krueger et al., 2007b). After presenting the activity (e.g., going out for dinner) and a pair of events (e.g. look at menu–order dinner), participants were asked to judge whether the pair was correctly ordered. The results showed that subregions of the mPFC (BA 10) were differentially engaged in mediating daily life activities depending on how often those were reportedly performed in daily life (Fig. 4a), confirming recent evidence that the mPFC is involved in mediating event sequence knowledge (Crozier et al., 1999; Knutson et al., 2004; Kuchinke et al., 2009; Partiot et al., 1996; Ruby et al., 2002). Importantly, the posterior medial part of BA 10 was activated for high frequency activities, whereas the anterior medial part of BA 10 was activated for low-frequency activities. Interestingly, each of the frequency-dependent mPFC regions falls onto one of the three architectonic subdivisions of the human BA 10 (Ongur et al., 2003) (Fig. 4b). These subregions have a similar cellular pattern, but vary in the degree of granularity and the development of cortical layer III (and layer IV), with the most prominent and well-developed layer III located in the polar area (10p), which is not observed in non-human primates (Creutzfeldt, 1995). This increase in cytoarchitectonic complexity along the rostro-caudal axis of the mPFC towards the frontopolar cortex might be an indication of the underlying frequency-dependent representation of event schemata encoded in each of the medial FC subregions. In conclusion, the evidence supports the assumption that the mPFC mediates event schemata that organize and guide the sequence for planning and performance of daily life activities. Being able to represent those schemata confer humans with a great advantage in carrying out plans, controlling a course of actions, or organizing everyday life routines.

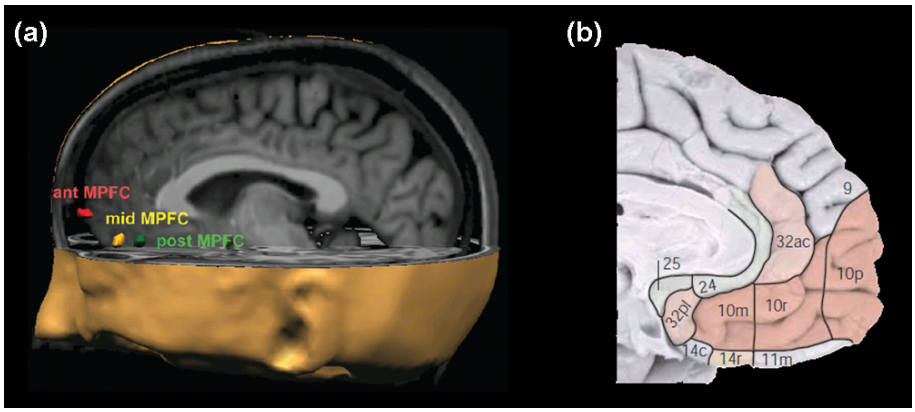

Figure 4. **Brain responses for daily life activities along the rostro-caudal mPFC axis**. (a) The posterior mPFC (post MPFC) was activated for high frequency activities, the middle mPFC (mid MPFC) for moderate frequency activities, and the anterior mPFC (ant MPFC) for low frequency activities. Adapted from Krueger et al., (2007b). (b) Location of cytoarchitectonic BA 10 surface-rendered onto medial surface of the human mPFC. Adapted from Ramnani and Owen (2004).

Experiment 2. The second fMRI study investigated the patterns of brain responses when participants were engaged in evaluating the complexity (i.e., number of events) of daily life activities selected on the basis of normative data (Krueger et al., 2009c). Participants were asked to rate daily life activity in terms of the number of events involved in the activity either consisting of few events (e.g., 'stirring a cup of coffee') or many events (e.g., 'planning a wedding'). The results revealed a left frontoparietal circuit expanding from the premotor cortex to the medial frontopolar cortex (posterior inferior parietal lobule, BA 39; premotor cortex, BA 6; dmPFC, BA 8; and medial FPC, BA 10) (Fig. 5a). As the left hemisphere is more adept at constructing determinate, precise, and unambiguous representations of the world (Beeman et al., 2000; Goel et al., 2007), it is designed to mediate the primary meaning of within-event information, sequential dependencies between single adjacent events, and coding of boundaries between events (Krueger and Grafman, 2008). Importantly, within the frontoparietal circuit the FPC (BA 10) was isolated as the only region that showed increased activation for more complex daily life activities (Fig. 5b). The FPC is ideally suited for representing more complex event schemata, because it is the single largest cytoarchitectonic area of the PFC (Ramnani and Owen, 2004) and among one of the last brain regions to mature (Diamond, 1991; Durston et al., 2001; Giedd et al., 1999; Sowell et al., 1999). In conclusion, the evidence supports the assumptions that the mFPC mediates event schemata that organize and guide the sequence for planning and performance of daily life activities. As one moves more rostrally within the mPFC, progressively more complex elators are represented that guide behavior over progressively longer temporal intervals. This type of knowledge provides the underlying cognitive structure for the human ability to build and execute complex behaviors ranging from carrying out simple plans to organizing complex daily life routines.

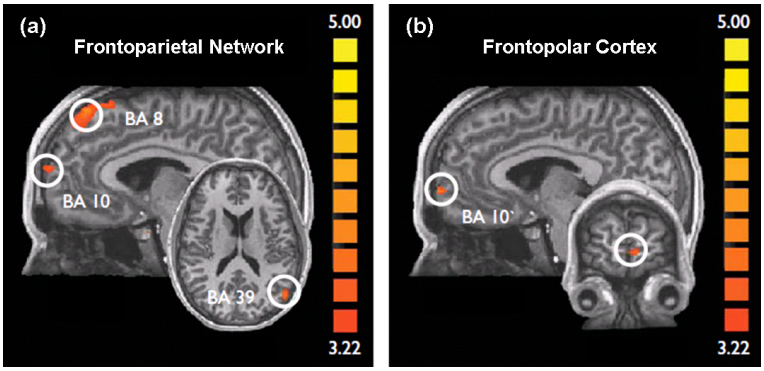

Figure 5. Brain responses for daily life complexity. (a) A left frontoparietal network (mPFC, BA 10; dmPFC, BA 8; premotor cortex, BA 6; and posterior inferior parietal lobule, BA 39) was activated by the complexity judgment task. (b) Activation in the frontopolar cortex increased for more complex daily life activities. Adapted from Krueger et al., (2009c).

Experiment 3. The final study combined functional and structural MRI to investigate the patterns of brain responses during imagination of daily life activities containing physical aggression and determined the cortical thickness in healthy male adolescents (Strenziok et al., 2009). Participants where asked to imagine their own aggressive behaviors during social interactions that were initiated by a fictitious male teenager that they incidentally met in a parking garage. The results revealed a co-localization of age-dependent activation changes and cortical thinning in the FPC, reflecting ongoing maturation of the FPC during adolescence towards a refinement of social information processing (Blakemore, 2008). Moreover, the results revealed reduced vmPFC activation while participants were mentally engaged in aggressive behavior to the extent to which adolescents experienced anger in everyday life (Fig. 6). Recent findings in adult patients with brain damage (Anderson et al., 1999; Blair and Cipolotti, 2000; Damasio et al., 1994; Grafman et al., 1996), aggressive populations (Koenigsberg et al., 2005; Soloff et al., 2000) and healthy adults (Pietrini et al., 2000) support this finding indicating that the vmPFC is critically involved in the control of aggressive behavior. Typically, the vmPFC modulates aggressive behaviors by exerting inhibitory control over aggressive impulses, however, this inhibitory control has to be loosened (associated with a dampening of vmPFC activation) to engage in imagined aggressive behavior. In conclusion, the evidence supports the assumptions that the mPFC mediates event schemata that organize and guide the sequence for performance of imagined aggressive behavior. Furthermore, the co-localization of age-dependent activation changes and cortical thinning indicates an ongoing maturation of the FPC during adolescence towards a refinement of social information processing that can potentially facilitate mature social behavior in aggressive contexts.

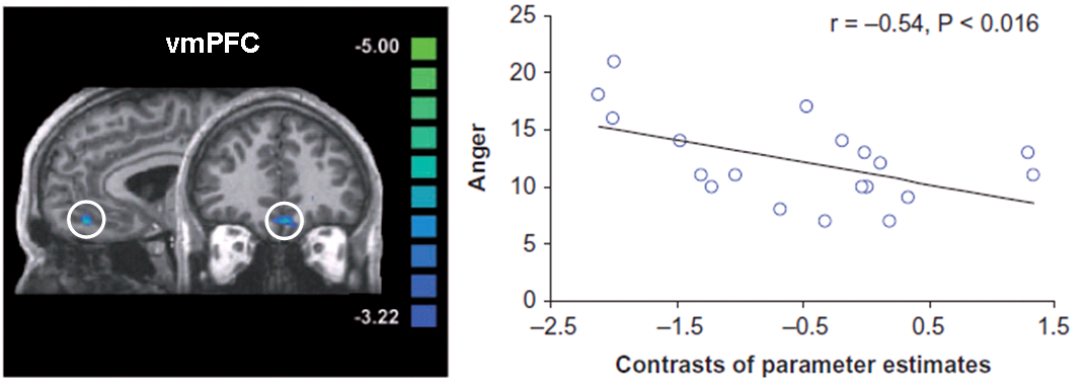

Figure 6. Brain responses during imagined aggression. The vmPFC showed reduced activation while participants were engaged in imagining aggressive behavior to the extent to which adolescent males experienced anger in everyday life. Adapted from Strenziok et al. (2009).

In summary, the evidence supports the prediction that the sequential knowledge component of social event knowledge is of crucial importance for event schemata. In particular, elators represented in the mPFC simulate event schemata that organize and guide the sequence for planning and performance of daily life routines. This evidence is further supported by clinical observations that damage to the mPFC leads to an inability to produce goal-directed behavior such as carrying out plans, controlling a course of actions, or organizing everyday life routines (Eslinger and Damasio, 1985; Janowsky et al., 1989; Shallice, 1982; Shallice and Burgess, 1991; Sirigu et al., 1996; Sirigu et al., 1995; Stuss and Benson, 1984). Finally, there exists further confirming evidence from a recent quantitative neuroimaging meta-analysis (Van Overwalle, 2008) showing that a broad range of social tasks such as social judgment about *(i) event knowledge, (ii) morality, (iii) social scripts, and (iv) theory of mind beliefs* elicit activations in the mPFC (Fig. 7). Importantly, based on the STRing theory, these different task activation patterns can be parsimoniously explained by reenactment of different components contained in social event knowledge: the action tasks draw on goals or end-states of agents or actions; the morality tasks on just or unjust actions of agents; the social script tasks on the sequence of events; and the theory of mind beliefs tasks on intentions and desires of agents. Moreover, the STRing theory predicts a segregation of elator functions along the dorso-ventral mPFC axis: goal knowledge mediated by the dmPFC pathway supports inferences about person schemata, whereas outcome knowledge mediated by the vmPFC/OFC pathway supports inferences about self schemata.

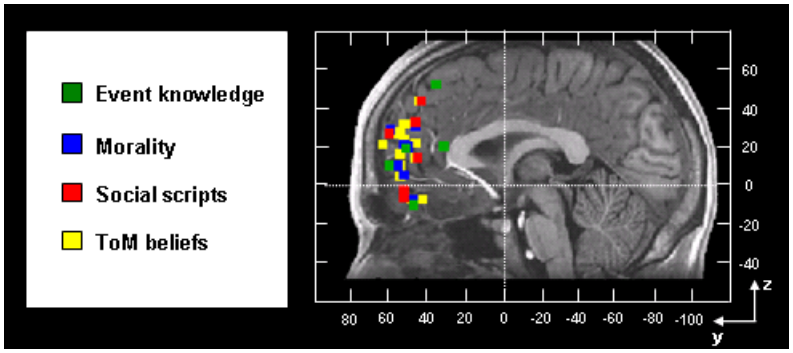

Figure 7. Neuroscience evidence in support for event schemata. Functional neuroimaging meta-analysis results are displayed for social judgment tasks about actions, morality, social scripts, and theory of mind (ToM) beliefs. Tasks reenacted elator components contained within event schemata and elicited activation in the mPFC. Adapted from van Overwalle (2008) and Krueger et al., (2009a); Talairach space: y-axis indicates anterior-posterior and z-axis inferior-superior.

Person Schemata. Person schemata describe conceptual structures of personality traits that enable a person to categorize and make inferences from the experiences of interactions with other people, and to anticipate the nature of interactions with individuals by providing control and predictability in social interactions (Cantor and Mischel, 1979). The STRing theory predicts that the *goal knowledge* component of social event knowledge is of crucial importance for person schemata: elators simulating person schemata preferentially recruit the dmPFC and reenactment of the goal pathway enables an agent to make inferences about the likely goals of other agents for goal achievement in social situations. To test this hypothesis, three neuroimaging experiments were performed to investigate the underlying neural structure of person schemata by *focusing on the goal knowledge component of social event knowledge*.

Experiment 1. The first fMRI study investigated the patterns of brain responses for conditional and unconditional trust during social exchange (Krueger et al., 2007a). Two strangers interacted with one another in a sequential multiround reciprocal trust game to make decisions for monetary payoffs. The results revealed that the dmPFC is critically involved in building a trust relationship by inferring another person's goals, determining whether to trust a person in the future (Gallagher et al., 2002; McCabe et al., 2001; Rilling et al., 2004) (Fig. 8a). Importantly, the result suggest that the dmPFC can be differently engaged to recruit more primitive neural systems in maintaining conditional and unconditional trust in a partnership (Fig. 8b). By adopting a conditional trust strategy, the defector group (in which partners experienced some defections during the experiment) showed a significant increase in dmPFC activation over the experiment and selectively activated the ventral tegmental area (VTA), a region linked to the dopaminergic mesolimbic reward system providing a general reinforcement mechanism to encode expected and realized reward (Andreasen et al., 1994; Fiorillo et al., 2003). In contrast, by adopting an unconditional trust strategy, the non-defector group (in which neither player ever defected on their partners' decision to trust) showed a significant decrease in dmPFC activation over the experiment and selectively activated the septal area (SA), a limbic brain region linked to modulate various aspects of social behavior including pair bonding, social recognition, and social attachment (Aron et al., 2005; Moll et al., 2006; Numan, 2000). In conclusion, the evidence supports the assumptions that the dmPFC mediates person schemata that enable an agent to make inferences about the likely goals of other agents during social interactions. As one of the distinguishing

features of the human species, this more recently evolved dmPFC region can be differently engaged via structural and temporal representation binding through the goal pathway with more primitive neural systems in maintaining conditional (VTA) and unconditional trust (SA) in a partnership.

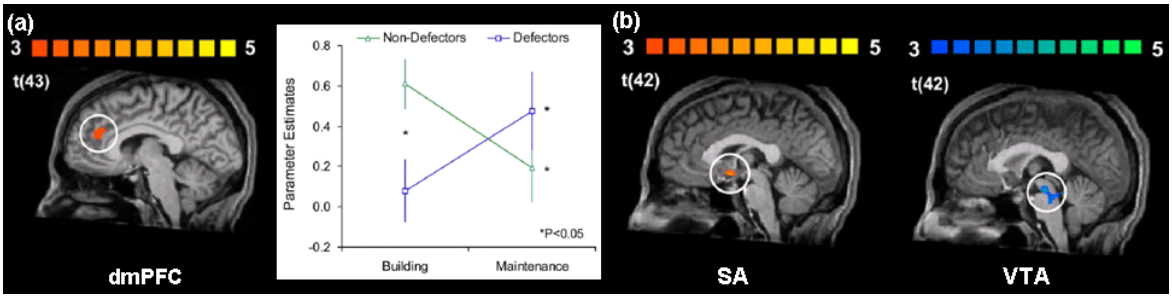

Figure 8. Brain responses for interpersonal trust. (a) Decisions to trust activated the dmPFC (BA 9/32). The non-defector group showed a decrease in dmPFC activation, whereas the defector group showed an increase in dmPFC activation across stages. (b) Different engagement of the dmPFC allowed recruiting of more primitive neural systems in maintaining unconditional (SA) and conditional (VTA) trust in a partnership. Adapted from Krueger et al., (2007a).

Experiment 2. The second fMRI study investigated the different patterns of brain responses for trusting versus reciprocating behavior during social exchange (Krueger et al., 2008). Two strangers interacted with one another in a sequential multiround reciprocal trust game while they were asked to make decisions for monetary payoffs. The results revealed that the dmPFC and anterior insula (AI) were commonly recruited for decisions to trust and reciprocate (Fig. 9a). The dmPFC plays a critical role in representing another person's psychological perspective allowing partners to predict the behavior of others by determining whether to trust their partners and whether their partners will reciprocate their trust in the future (Amodio and Frith, 2006). The AI region has been associated with empathy, which plays both an epistemological role to provide information about the future actions of other individuals and a social role to serve as the origin of the motivation for cooperative and pro-social behavior (de Vignemont and Singer, 2006). Importantly, the results further demonstrated that the FPC and the right temporoparietal junction (TPJ) were specifically recruited for decisions to trust (Fig. 9b). The right TPJ is engaged in perspective taking helping to distinguish between self- and other-related behavior (Decety and Lamm, 2007; Mitchell, 2008), whereas the FPC encodes meta-cognitive representations that enable humans to reflect on long-term goals (Tanaka et al., 2004; Wood and Grafman, 2003). In conclusion, the evidence supports the assumption that dmPFC mediates person schemata that enable an agent to make

inferences about the likely goals of other agents and to anticipate long-term goals and outcomes of future interactions with other agents. Trusting and reciprocating behavior draws upon recently evolved neural systems via structural and temporal representation binding through the goal pathway with regions in the posterior cerebral cortex (e.g., TPJ) and subcortical brain structures (AI) supporting reciprocal exchange and producing mutual advantage that operates beyond the immediate spheres of kinship.

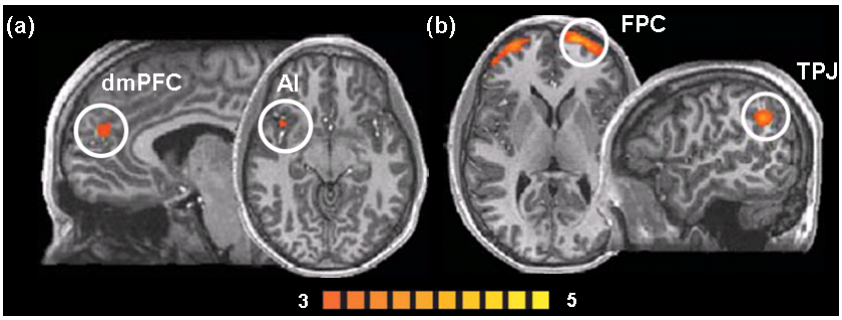

Figure 9. Brain responses for trust and reciprocity. (a) The dmPFC (BA 9/32) and the AI (BA 13) were commonly activated for trusting and reciprocating behavior. (b) Decisions to trust specifically activated the bilateral FPC (BA 10) and right TPJ (BA 40). Adapted from Krueger et al., (2008).

Experiment 3. The final fMRI study investigated the underlying neural structure of social concepts such as 'tactless' or 'honorable', which allow us to describe other agents' social behaviors (Zahn et al., 2007). Participants were asked to make judgments about the meaning relatedness of word pairs of social concepts (e.g., honor–brave). The results showed that judgment of social concepts activated the dmPFC (BA 10/32) (Fig. 10a), and activation in the anterior temporal pole (aTP, BA 38) was correlated with the richness of detail with which social concepts describe social behavior (Fig. 10b). The results agree with the central role for the dmPFC for inferring another person's intentions to predicting social behaviors (Amodio and Frith, 2006; Gusnard et al., 2001) and for the aTP for representing conceptual knowledge (Davies et al., 2005; Garrard and Carroll, 2006; McClelland and Rogers, 2003). Although previous studies have shown subdivisions for different semantic domains (e.g., tools, animals, and faces) in modality-specific posterior temporal regions (Chao et al., 1999; Ishai et al., 1999), this study demonstrated that specialized subregions for different social conceptual domains also exist within the aTP. In conclusion, the evidence supports the assumptions that the dmPFC mediates person schemata that enable an agent to make inferences about the likely goals of other agents. As a unique feature of humans, the dmPFC (representing social event knowledge) interacts with the aTP (representing social concept knowledge)

via structural and temporal representation binding through the goal pathway to enable the description of another person's social behavior.

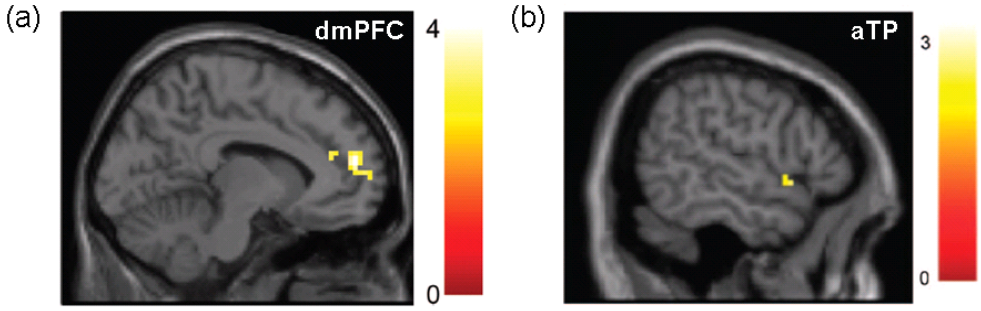

Figure 10. Brain responses for social concepts. (a) Judgment of social concepts revealed activation in the dmPFC (BA 10/32). (b) The right aTP (BA 38) was correlated with the richness of detail with which social concepts describe social behavior. Adapted from Zahn et al., (2007).

In summary, the evidence confirms that the goal knowledge component of social event knowledge is of crucial importance for person schemata. Elators simulating person schemata preferentially recruited the dmPFC and reenactment of the goal pathway enabled an agent to make inferences about the likely goals of other agents in social situations. This evidence is further supported by a recent quantitative neuroimaging meta-analysis (Van Overwalle, 2008) (Fig. 11). The results showed that inferences about the person schemata —individuals made judgments about goal knowledge that enables an inference about the goal-directed actions of others derived from behavior in short stories, sentences, and single words, or interactive neuroeconomic games— preferentially activated the dmPFC. In addition, there exist confirming evidence that damage to the dmPFC leads to an inability to infer about goal-directed behaviors of others during social exchange (Kain and Perner, 2003; Manes et al., 2002; Stuss et al., 2001).

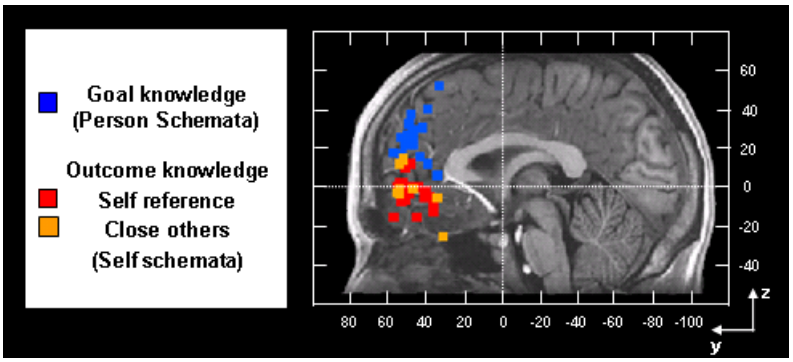

Figure 11. Neuroscience Evidence in Support for Person and Self Schemata. Functional neuroimaging meta-analysis results are displayed for tasks that reenact elator components contained within person and self schemata. Goal knowledge supports inferences about person schemata and preferentially recruits the dmPFC. Outcome knowledge enables inferences about self schemata and preferentially recruits the vmPFC. Adapted from van Overwalle (2008) and Krueger et al., (2009a); Talairach space: y-axis indicates anterior-posterior and z-axis inferior-superior lines.

Self schemata. Self schemata refer to cognitive generalizations about the self derived from past experience that organize and guide the processing of self-related information contained in the individual's social experience (Markus, 1977). The STRing theory predicts that the *outcome knowledge* component of social event knowledge is of crucial importance for self schemata: elators simulating self schemata preferentially recruit the vmPFC and reenactment of the outcome pathway enables inferences about the likely affective responses and reward values accompanying self-related information processing. To test this hypothesis, three neuroimaging experiments were performed to investigate the underlying neural structure of self schemata by *focusing on the outcome knowledge component of social event knowledge*.

Experiment 1. The first study combined multidimensional scaling (MDS) and parametric fMRI to investigate how the underlying psychological architecture of political beliefs is structured and where the multidimensional structure of political beliefs is represented in the brain (Zamboni et al., 2009). Participants were asked to judge whether they agree or disagree with short political statements (e.g., The government should invest more in welfare.). The results revealed three independent dimensions of political beliefs: individualism, conservatism, and radicalism (Fig. 12a). Each dimension was reflected in a distinctive pattern of neural activations: (i) individualism (vmPFC, dmPFC, TPJ), (ii) conservatism (dlPFC), and (iii) radicalism (ventral striatum and precuneus), known to be involved in self-other processing (Mitchell et al., 2006), social decision-making in ambivalent situations (Kaplan et al., 2007; Knutson et al., 2006), and reward prediction (Rilling et al., 2002; Schultz et al., 1998), respectively. For the individualism (self vs. other) dimension, the TPJ plays a key role in perspective taking helping to distinguish between self- and other-related behavior (Decety and Lamm, 2007; Decety and Sommerville, 2003) (Fig. 12b). Importantly, more individual-centered political statements (e.g., Everybody should prioritize his or here own interest over society's.) were associated with greater vmPFC activity due to more self-referential social processing (Mitchell et al., 2006; Northoff et al., 2006). In contrast, more society-centered statements (e.g., Citizen should vote based on collective interest.) were associated with greater dmPFC activity due to more others-related social processing (Amodio and Frith, 2006; Mitchell et al., 2006). In conclusion, the evidence supports the assumptions that the vmPFC mediates self schemata via reenactment of the outcome pathway that organize and guide the processing of self-related information reflected in

political beliefs. As a fundamental human aspect, multidimensional political belief systems evolved from more basic social processes through which individuals interact to reach consensus in society.

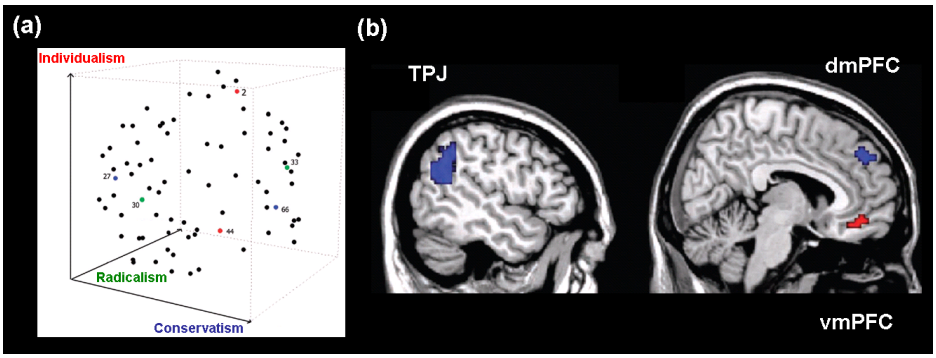

Figure 12. Structure and neural correlates of political beliefs. (a) The MDS analysis revealed a three-dimensional spatial distribution for which each political statement can be described by three coordinates (x = conservatism, y = individualism, z = radicalism). (b) For the individualism dimension, the dmPFC and TPJ were increasingly activated by more society-related statements (shown in blue), whereas the vmPFC was increasingly activated by more individual-related statements (shown in red). Adapted from Zamboni et al., (2009).

Experiment 2. The second fMRI study investigated the patterns of brain responses for charitable donation as an outstanding example of human altruism (Moll et al., 2006). Participants chose to endorse or oppose societal causes by anonymous decisions to donate or refrain from donating to real charitable organizations lined to a wide range of societal causes (e.g., abortion, death penalty, euthanasia). The results revealed, compatible with the 'warm glow' (joy of giving) effect (Andreoni, 1990), that donating to societal causes as well as earning money share the same neural systems of reward reinforcement and expectancy (ventral tegmental area, VTA; dorsal and ventral striatum, STR) (O'Doherty et al., 2006; Schultz et al., 1997), (Fig. 13a). The subgenual (SG) and lateral OFC (lOFC) areas were activated for decisions to donate or to oppose societal causes, playing key roles in more primitive mechanisms of social attachment (Bartels and Zeki, 2004; Young and Wang, 2004) and aversion (Blair et al., 1999; Kringelbach, 2005), respectively (Fig. 13b). Importantly, the anterior part of the vmPFC (aPFC) was recruited when altruistic choices prevail over selfish material interests to the extent to which individuals were engaged in real-life voluntary charitable activities (Fig. 13c). The results are in agreement with the central role of the aPFC in altruistic punishment (de Quervain et al., 2004), prediction of future rewards (Rilling et al., 2002; Schultz et al., 1997), and moral appraisals (Moll et al., 2002; Singer et al., 2004). In conclusion, the evidence supports the assumptions that the vmPFC mediates self schemata that organize

and guide the processing of self-related information reflected in altruistic behavior via the outcome pathway with general mammalian neural systems of reward, social attachment, and aversion. As a consequence, human altruism is able far to exceed the immediate bonds of kinship, even when no material or reputation gains are anticipated.

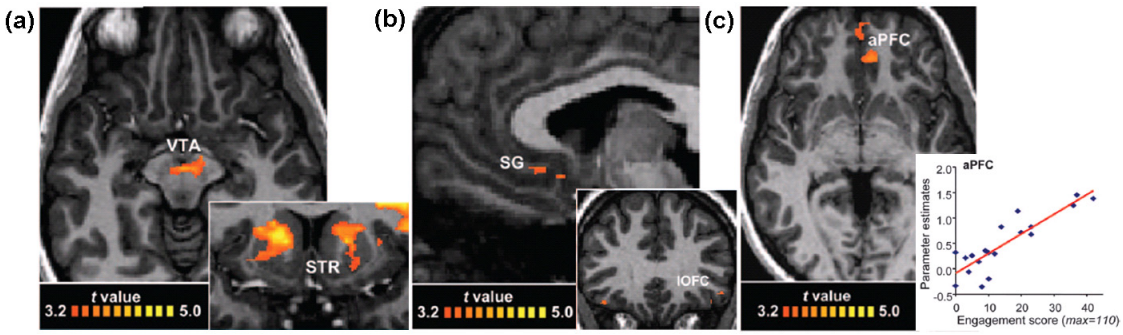

Figure 13. Brain responses for monetary reward and donation. (a) The mesolimbic–striatal reward system (VTA, STR) was activated for both pure monetary reward and non-costly donation. (b) Decisions to donate or to oppose societal cause activated SG and lOFC areas, respectively. (c) The aPFC was distinctively activated when altruistic choices prevail over selfish material interests. Activation of aPFC was correlated with self-reported ratings of engagement in real-life voluntary charitable activities. Adapted from Moll et al., (2006).

Experiment 3. The final study investigated the underlying neural structure of emotional intelligence in a sample of combat veterans from the Vietnam Head Injury Study, which is a prospective, long-term follow-up study of veterans with focal penetrating head injuries. Veterans were divided into vmPFC and dlPFC lesion (experimental) groups and a non-head-injured group (control, NC) based upon the presence or absence of local penetrating head injuries due to low velocity shrapnel wounds. The Mayer-Salovey-Caruso Emotional Intelligence Test was administered to examine strategic emotional intelligence (i.e., competency to understand emotional information and to apply it for the management of the self) and experiential (i.e., competency to perceive emotional information and to apply it for the integration into thinking) emotional intelligence (Mayer et al., 2008; Mayer et al., 2003). The results revealed vmPFC damage diminished strategic emotional intelligence and hinders the understanding of emotional information to apply it for the management of the self, whereas dlPFC damage diminished experiential emotional intelligence and hinders the perception of emotional information (Fig. 14). Importantly, since the vmPFC is interconnected with limbic structures critical for long-term memory and the processing of internal states (affect and motivation) (Barbas and De Olmos, 1990; Porrino et al., 1981), it is well suited for processing knowledge that is crucial for understanding and managing emotionally relevant information of the self (Bar-On et al., 2003; Damasio, 1996). Convergent evidence has

shown that vmPFC damage leads to problems in interpersonal interactions and abnormal changes in personality (Beer et al., 2003; Eslinger and Damasio, 1985) as well as diminished capacities to respond to emotional values attributed to rewards and punishment (Bechara et al., 1997; Kringelbach, 2005). In conclusion, the evidence supports the assumptions that the vmPFC mediates self schemata via reenactment of the outcome pathway that organize and guide the processing of self-related information reflected in emotional intelligence. Emotional intelligence should be viewed as complementary to cognitive intelligence and, when considered together, will provide a more complete understanding of human social behavior.

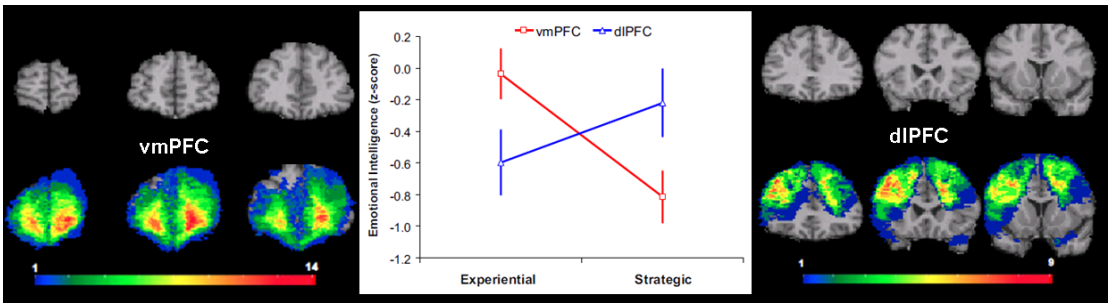

Figure 14. Neural substrates of emotional intelligence. Coronal views are shown for the vmPFC (left) and dlPFC (right) group lesion overlaps. The color indicates the number of individuals with damage to a given voxel. The experiential and strategic emotional intelligence scores of the dlPFC and vmPFC groups were normalized (z-transformation) in comparison to the performances of the NC group. The results indicate a double dissociation in patient's EI performances. Adapted from Krueger et al., (2009b).

In summary, the evidence confirms that the outcome knowledge component of social event knowledge is of crucial importance for self schemata. Elators simulating self schemata preferentially recruited the vmPFC and reenactment of the outcome pathway enabled inferences about the likely affective responses and reward values accompanying self-related information processing. Beside the provided evidence the proposed segregation of elator functions is further supported by a recent quantitative neuroimaging meta-analysis (Van Overwalle, 2008) (Fig. 11). The results showed inferences about the self schemata —individuals made judgments about event outcomes that enable an inference about the affective states and rewards associated with goal achievement in retrospective to one-self or close others (e.g., mother and friends) in the form of ratings and descriptions, memories about the self, and thinking about one's hopes— preferentially activated the vmPFC/mOFC. Finally, confirming evidence exist that damage to the vmPFC/mOFC leads to an inability to develop a coherent model of one's

own self with subsequent emotional lability (Damasio, 1999; Schore, 2003) and to severe impairment of social behavior such as social inappropriateness, lack of insight and initiative, poor judgment, and inappropriate affect (Anderson et al., 1999; Barrash et al., 2000; Eslinger et al., 1992; Masterman and Cummings, 1997). Note that it is not by chance that affect and reward are regarded as key components for self schemata. Anatomically, the 'core self' has been associated with the vmPFC/mOFC (Decety and Sommerville, 2003; Northoff and Bermpohl, 2004), because affect and reward are crucial to efficiently guide an individual's decision-making during social conduct (Rolls, 1999; Tremblay and Schultz, 2000).

1.4 Conclusion

Based on the evolution and biology of the human PFC, I developed an integrative theory of the cognitive and neural basis of social event knowledge. The STRing theory assumes that the human mPFC represents elators that encompass a multi-modal representation of social event knowledge distributed throughout the brain's association and modality-specific areas. Once an elator exists, it can reenact small subsets of its content as specific elations. Elators as abstract dynamic structured summary representations provide the underlying properties for social cognitive structures such as event schemata, person schemata, and self schemata that are intimately involved in planning and monitoring one's own behavior as well as understanding and predicting the behavior of others. Elators can be seen as shared representations that have the capacity to coordinate first-person and third-person information via a single conceptual system, which allows us to understand other's behavior by virtue of understanding our own behavior.

Consistent with neuroscience evidence, I proposed a segregation of elator functions along the dorso-ventral mPFC axis: goal knowledge mediated by the dmPFC pathway supports inferences about the likely actions performed by agents for goal achievement, whereas outcome knowledge mediated by the vmPFC/mOFC pathway supports inferences about the likely affective responses and reward value accompanying goal achievement. Most rostral parts of the mPFC mediate more complex organized elators that allow integration over progressively longer temporal intervals of information from the goal pathway with information from the outcome pathway. The STRing theory generates testable hypotheses, anatomically and functionally specifies the nature of the information being processed, and poses new questions for empirical research. For

example, what is the role of subcomponents of social event knowledge within the left and right hemispheres of the brain, given that the left PFC is more adept at constructing determinate, precise, and unambiguous representations of the world, whereas the right PFC is more adept at constructing and maintaining fluid, indeterminate, vague, and ambiguous representations of the world (Beeman et al., 2000; Goel et al., 2007)? Moreover, what underlying brain mechanisms for the proposed social functions are involved when individuals have not established relevant dynamic structured summary representations such as in the case of social brain disorders (e.g., autistic spectrum disorders)? From my perspective, studying the nature of dynamic structured summary representations is a fruitful way to characterize and identify the neural basis that underlies uniquely human social cognitive abilities, through patient studies and neuroimaging. Defining social functions that can be reconciled with the brain's anatomical and physiological properties can bring us one step closer to an understanding of the contribution of the PFC to uniquely human social behavior.

2. References

Adolphs R. Cognitive neuroscience of human social behaviour. Nat Rev Neurosci 2003; 4: 165-78.

Alexander GE, Crutcher MD, DeLong MR. Basal ganglia-thalamocortical circuits: parallel substrates for motor, oculomotor, "prefrontal" and "limbic" functions. Prog Brain Res 1990; 85: 119-46.

Amodio DM, Frith CD. Meeting of minds: the medial frontal cortex and social cognition. Nat Rev Neurosci 2006; 7: 268-77.

Anderson SW, Bechara A, Damasio H, Tranel D, Damasio AR. Impairment of social and moral behavior related to early damage in human prefrontal cortex. Nat Neurosci 1999; 2: 1032-7.

Andreasen NC, Nopoulos P, Schultz S, Miller D, Gupta S, Swayze V, et al. Positive and negative symptoms of schizophrenia: past, present, and future. Acta Psychiatr Scand Suppl 1994; 384: 51-9.

Andreoni J. Impure Altruism and Donations to Public Goods: A Theory of Warm-Glow Giving. Eco J 1990; 100: 464-477.

Aron A, Fisher H, Mashek DJ, Strong G, Li H, Brown LL. Reward, motivation, and emotion systems associated with early-stage intense romantic love. J Neurophysiol 2005; 94: 327-37.

Badre D. Cognitive control, hierarchy, and the rostro-caudal organization of the frontal lobes. Trends Cogn Sci 2008; 12: 193-200.

Bar-On R, Tranel D, Denburg NL, Bechara A. Exploring the neurological substrate of emotional and social intelligence. Brain 2003; 126: 1790-800.

Barbas H. Complementary roles of prefrontal cortical regions in cognition, memory, and emotion in primates. Adv Neurol 2000; 84: 87-110.

Barbas H, De Olmos J. Projections from the amygdala to basoventral and mediodorsal prefrontal regions in the rhesus monkey. J Comp Neurol 1990; 300: 549-71.

Barbas H, Ghashghaei H, Dombrowski SM, Rempel-Clower NL. Medial prefrontal cortices are unified by common connections with superior temporal cortices and distinguished by input from memory-related areas in the rhesus monkey. J Comp Neurol 1999; 410: 343-67.

Barbey AK, Krueger F, Grafman J. An evolutionarily adaptive neural architecture for social reasoning. Trends Neurosci 2009.

Barrash J, Tranel D, Anderson SW. Acquired personality disturbances associated with bilateral damage to the ventromedial prefrontal region. Dev Neuropsychol 2000; 18: 355-81.

Barresi J, Moore C. Intentional relations and social understanding. Behav Brain Sci 1996; 19: 107-154.

Barsalou LW. Perceptual symbol systems. Behavioral and Brain Sciences 1999; 22: 577-609.

Barsalou LW. Abstraction in perceptual symbol systems. Philos Trans R Soc Lond B Biol Sci 2003; 358: 1177-87.

Barsalou LW. Cognitive and neural contributions to understanding the conceptual system. Curr Dir Psych Sci 2008a; 17: 91-95.

Barsalou LW. Grounded cognition. Annu Rev Psychol 2008b; 59: 617-45.

Barsalou LW, Breazeal C, Smith LB. Cognition as coordinated non-cognition. Cogn Process 2007; 8: 79-91.

Barsalou LW, Niedenthal PM, Barbey A, Ruppert J. Social embodiment. In: Ross B, editor. The Psychology of Learning and Motivation. Vol 43. San Diego: Academic Press, 2003: 43-92.

Bartels A, Zeki S. The neural correlates of maternal and romantic love. Neuroimage 2004; 21: 1155-66.

Bechara A, Damasio H, Tranel D, Damasio AR. Deciding advantageously before knowing the advantageous strategy. Science 1997; 275: 1293-5.

Beeman MJ, Bowden EM, Gernsbacher MA. Right and left hemisphere cooperation for drawing predictive and coherence inferences during normal story comprehension. Brain Lang 2000; 71: 310-36.

Beer JS, Heerey EA, Keltner D, Scabini D, Knight RT. The regulatory function of self-conscious emotion: insights from patients with orbitofrontal damage. J Pers Soc Psychol 2003; 85: 594-604.

Blair RJ, Cipolotti L. Impaired social response reversal. A case of 'acquired sociopathy'. Brain 2000; 123 (Pt 6): 1122-41.

Blair RJ, Morris JS, Frith CD, Perrett DI, Dolan RJ. Dissociable neural responses to facial expressions of sadness and anger. Brain 1999; 122 (Pt 5): 883-93.

Blakemore SJ. The social brain in adolescence. Nat Rev Neurosci 2008; 9: 267-77.

Botvinick MM. Hierarchical models of behavior and prefrontal function. Trends Cogn Sci 2008; 12: 201-8.

Brodmann K. Neue Ergebnisse ueber die vergleichende histologische Lokalisation der Grosshirnrinde mit besonderer Beruecksichtigung des Stirnhirns. Anat. Anz. Suppl 1912; 41: 157-216.

Byrne R, Whiten A. Machiavellian intelligence. Oxford: Oxford University Press, 1988.

Cantor N, Mischel W. Prototypes in person perception. Adv Exp Soc Psychol 1979; 12: 4-47.

Carmichael ST, Price JL. Connectional networks within the orbital and medial prefrontal cortex of macaque monkeys. J Comp Neurol 1996; 371: 179-207.

Chao LL, Haxby JV, Martin A. Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. Nat Neurosci 1999; 2: 913-9.

Chiavaras MM, LeGoualher G, Evans A, Petrides M. Three-dimensional probabilistic atlas of the human orbitofrontal sulci in standardized stereotaxic space. Neuroimage 2001; 13: 479-96.

Christoff K, Gabrieli DE. The frontopolar cortex and human cognition: Evidence for a rostrocaudal hierarchical organziation within the human prefrontal cortex. Psychobiology 2000; 28: 168-186.

Chugani HT, Phelps ME, Mazziotta JC. Positron emission tomography study of human brain functional development. Ann Neurol 1987; 22: 487-97.

Conel JL. The Postnatal Development of the Human Cerebral Cortex. Vol 1-6. Cambridge, MA: Havard Universtiy Press, 1939.

Creutzfeldt O. Cortex cerebri: performance, structural and functional organization of the cortex. Oxford: Oxford University Press, 1995.

Crozier S, Sirigu A, Lehericy S, van de Moortele PF, Pillon B, Grafman J, et al. Distinct prefrontal activations in processing sequence at the sentence and script level: an fMRI study. Neuropsychologia 1999; 37: 1469-76.

Damasio AR. Time-locked multiregional retroactivation: a systems-level proposal for the neural substrates of recall and recognition. Cognition 1989; 33: 25-62.

Damasio AR. The somatic marker hypothesis and the possible functions of the prefrontal cortex. Philos Trans R Soc Lond B Biol Sci 1996; 351: 1413-20.

Damasio AR. The Feeling of What Happens: Body and Emotion in the Making of Consciousness Orlando, FL: Harcourt, 1999.

Damasio H, Grabowski T, Frank R, Galaburda AM, Damasio AR. The return of Phineas Gage: clues about the brain from the skull of a famous patient. Science 1994; 264: 1102-5.

Davies RR, Hodges JR, Kril JJ, Patterson K, Halliday GM, Xuereb JH. The pathological basis of semantic dementia. Brain 2005; 128: 1984-95.

de Quervain DJ, Fischbacher U, Treyer V, Schellhammer M, Schnyder U, Buck A, et al. The neural basis of altruistic punishment. Science 2004; 305: 1254-8.

de Vignemont F, Singer T. The empathic brain: how, when and why? Trends Cogn Sci 2006; 10: 435-41.

Decety J, Lamm C. The role of the right temporoparietal junction in social interaction: how low-level computational processes contribute to meta-cognition. Neuroscientist 2007; 13: 580-93.

Decety J, Sommerville JA. Shared representations between self and other: a social cognitive neuroscience view. Trends Cogn Sci 2003; 7: 527-33.

Diamond A. Guidelines for the study of brain-behavior relationships during development. In: Levin HS, Eisenberg A and Benton AL, editors. Frontal Lobe Function and Dysfunction. New York: Oxford University Press, 1991.

Dunbar RIM. The social brain hypothesis. Evol Anthrop 1998; 6: 178-190.

Duncan J. An adaptive coding model of neural function in prefrontal cortex. Nat. Rev. Neurosci. 2001; 2: 820-9.

Durston S, Hulshoff Pol HE, Casey BJ, Giedd JN, Buitelaar JK, van Engeland H. Anatomical MRI of the developing human brain: what have we learned? J Am Acad Child Adolesc Psychiatry 2001; 40: 1012-20.

Elliott R, Dolan RJ, Frith CD. Dissociable functions in the medial and lateral orbitofrontal cortex: evidence from human neuroimaging studies. Cereb Cortex 2000; 10: 308-17.

Elston GN. Pyramidal cells of the frontal lobe: all the more spinous to think with. J Neurosci 2000; 20: RC95.

Elston GN, Rosa MG. Pyramidal cells, patches, and cortical columns: a comparative study of infragranular neurons in TEO, TE, and the superior temporal polysensory area of the macaque monkey. J Neurosci 2000; 20: RC117.

Engel AK, Singer W. Temporal binding and the neural correlates of sensory awareness. Trends Cogn Sci 2001; 5: 16-25.

Eslinger PJ, Damasio AR. Severe disturbance of higher cognition after bilateral frontal lobe ablation: patient EVR. Neurology 1985; 35: 1731-41.

Eslinger PJ, Grattan LM, Damasio H, Damasio AR. Developmental consequences of childhood frontal lobe damage. Arch Neurol 1992; 49: 764-9.

Fiorillo CD, Tobler PN, Schultz W. Discrete coding of reward probability and uncertainty by dopamine neurons. Science 2003; 299: 1898-902.

Fiske ST, Taylor SE. Social Cognition New York: McGraw-Hill, 1991.

Flechsig P. Anatomie des menschlichen Gehirns und Rueckenmarks auf myelogenetischer Grundlage. Leipzig: Thieme, 1920.

Frith CD, Frith U. The neural basis of mentalizing. Neuron 2006; 50: 531-4.

Fuster JM. The prefrontal cortex: Anatomy, physiology, and neuropsychology of the frontal lobe. New York: Raven Press, 1997.

Fuster JM. The prefrontal cortex--an update: time is of the essence. Neuron 2001; 30: 319-33.

Fuster JM, Alexander GE. Neuron activity related to short-term memory. Science 1971; 173: 652-654.

Gallagher HL, Jack AI, Roepstorff A, Frith CD. Imaging the intentional stance in a competitive game. Neuroimage 2002; 16: 814-21.

Garrard P, Carroll E. Lost in semantic space: a multi-modal, non-verbal assessment of feature knowledge in semantic dementia. Brain 2006; 129: 1152-63.

Giedd JN, Blumenthal J, Jeffries NO, Castellanos FX, Liu H, Zijdenbos A, et al. Brain development during childhood and adolescence: a longitudinal MRI study. Nat Neurosci 1999; 2: 861-3.

Gilbert SJ, Spengler S, Simons JS, Frith CD, Burgess PW. Differential functions of lateral and medial rostral prefrontal cortex (area 10) revealed by brain-behavior associations. Cereb Cortex 2006a; 16: 1783-9.

Gilbert SJ, Spengler S, Simons JS, Steele JD, Lawrie SM, Frith CD, et al. Functional specialization within rostral prefrontal cortex (area 10): a meta-analysis. J Cogn Neurosci 2006b; 18: 932-48.

Goel V, Tierney M, Sheesley L, Bartolo A, Vartanian O, Grafman J. Hemispheric specialization in human prefrontal cortex for resolving certain and uncertain inferences. Cereb Cortex 2007; 17: 2245-50.

Grafman J. Similarities and distinctions among current models of prefrontal cortical functions. In: Grafman J, Holyoak KJ and Boller F, editors. Structure and functions of the human prefrontal cortex. New York: New York Academy of Sciences, 1995: 337-368.

Grafman J, Schwab K, Warden D, Pridgen A, Brown HR, Salazar AM. Frontal lobe injuries, violence, and aggression: a report of the Vietnam Head Injury Study. Neurology 1996; 46: 1231-8.

Groenewegen HJ, Uylings HB. The prefrontal cortex and the integration of sensory, limbic and autonomic information. Prog Brain Res 2000; 126: 3-28.

Gusnard DA, Akbudak E, Shulman GL, Raichle ME. Medial prefrontal cortex and self-referential mental activity: relation to a default mode of brain function. Proc Natl Acad Sci U S A 2001; 98: 4259-64.

Heberlein AS. Animacy and intention in the brain: Neuroscience of social event perception. In: Shipley T and Zacks JM, editors. Understanding events: From perception to action. Oxford: Oxford University Press, 2008: 363-388.

Huey ED, Krueger F, Grafman J. Representations in the Human Prefrontal Cortex. Curr Dir Psych Sci 2006; 15: 167-171.

Humphreys N. The social function of intellect. In: Bateson P and HInde R, editors. Growing points in ethology. Cambridge: Cambridge University Press, 1976: 303-317.

Huttenlocher PR. Morphometric study of human cerebral cortex development. Neuropsychologia 1990; 28: 517-27.

Huttenlocher PR, Dabholkar AS. Regional differences in synaptogenesis in human cerebral cortex. J Comp Neurol 1997; 387: 167-78.

Ishai A, Ungerleider LG, Martin A, Schouten JL, Haxby JV. Distributed representation of objects in the human ventral visual pathway. Proc Natl Acad Sci U S A 1999; 96: 9379-84.

Janowsky JS, Shimamura AP, Squire LR. Source memory impairment in patients with frontal lobe lesions. Neuropsychologia 1989; 27: 1043-56.

Jolly A. Lemur social behavior and primate intelligence. Science 1966; 153: 501-6.

Kain W, Perner J. Do Children with ADHD not need their frontal lobes for theory of mind? A review of brain imaging and neuropsychological studies. In: Bruene M, Ribbert H and Schiefenhoevel W, editors. The social brain: Evolution and pathology. Hoboken, NJ: Wiley, 2003: 197-230.

Kaplan JT, Freedman J, Iacoboni M. Us versus them: Political attitudes and party affiliation influence neural response to faces of presidential candidates. Neuropsychologia 2007; 45: 55-64.

Knutson KM, Wood JN, Grafman J. Brain activation in processing temporal sequence: an fMRI study. Neuroimage 2004; 23: 1299-307.

Knutson KM, Wood JN, Spampinato MV, Grafman J. Politics on the Brain: An fMRI Investigation. Soc Neurosci 2006; 1: 25-40.

Koechlin E, Corrado G, Pietrini P, Grafman J. Dissociating the role of the medial and lateral anterior prefrontal cortex in human planning. Proc Natl Acad. Sci U S A 2000; 97: 7651-6.

Koechlin E, Summerfield C. An information theoretical approach to prefrontal executive function. Trends Cogn Sci 2007; 11: 229-35.

Koenigsberg HW, Buchsbaum MS, Buchsbaum BR, Schneiderman JS, Tang CY, New A, et al. Functional MRI of visuospatial working memory in schizotypal personality disorder: a region-of-interest analysis. Psychol Med 2005; 35: 1019-30.

Kringelbach ML. The human orbitofrontal cortex: linking reward to hedonic experience. Nat Rev Neurosci 2005; 6: 691-702.

Krueger F. Coding of temporal relations in semantic memory. Cognitive load and task-evoked pupillary response. Berlin: Waxman, 2000.

Krueger F, Barbey AK, Grafman J. The medial prefrontal cortex mediates social event knowledge. Trends Cogn Sci 2009a; 13: 103-109.

Krueger F, Barbey AK, McCabe K, Strenziok M, Zamboni G, Solomon J, et al. The neural bases of key competencies of emotional intelligence. Proc Natl Acad Sci U S A 2009b; 106: 22486-91.

Krueger F, Grafman J. The human prefrontal cortex stores structured event complexes. In: Shipley T and Zacks JM, editors. Understanding Events: From perception to action. Oxford: Oxford University Press, 2008: 617-638.

Krueger F, Grafman J, McCabe K. Review. Neural correlates of economic game playing. Philos Trans R Soc Lond B Biol Sci 2008; 363: 3859-3874.

Krueger F, McCabe K, Moll J, Kriegeskorte N, Zahn R, Strenziok M, et al. Neural correlates of trust. Proc Natl Acad Sci U S A 2007a; 104: 20084-9.

Krueger F, Moll J, Zahn R, Heinecke A, Grafman J. Event frequency modulates the processing of daily life activities in human medial prefrontal cortex. Cereb Cortex 2007b; 17: 2346-2353.

Krueger F, Spampinato MV, Barbey AK, Huey ED, Morland T, Grafman J. The frontopolar cortex mediates event knowledge complexity: a parametric functional MRI study. Neuroreport 2009c; 20: 1093-7.

Kuchinke L, Meer E, Krueger F. Differences in processing of taxonomic and sequential relations in semantic memory: an fMRI investigation. Brain Cogn 2009; 69: 245-51.

Levy R, Goldman-Rakic PS. Segregation of working memory functions within the dorsolateral prefrontal cortex. Exp Brain Res 2000; 133: 23-32.

Lieberman MD. Social cognitive neuroscience: a review of core processes. Annu Rev Psychol 2007; 58: 259-89.

Manes F, Sahakian B, Clark L, Rogers R, Antoun N, Aitken M, et al. Decision-making processes following damage to the prefrontal cortex. Brain 2002; 125: 624-39.

Markus H. Self-schemata and processing information about the self. J Pers Soc Psychol 1977; 35: 63-78.

Masterman DL, Cummings JL. Frontal-subcortical circuits: the anatomic basis of executive, social and motivated behaviors. J Psychopharmacol 1997; 11: 107-14.

Mayer JD, Salovey P, Caruso DR. Emotional intelligence: new ability or eclectic traits? Am Psychol 2008; 63: 503-17.

Mayer JD, Salovey P, Caruso DR, Sitarenios G. Measuring emotional intelligence with the MSCEIT V2.0. Emotion 2003; 3: 97-105.

McCabe K, Houser D, Ryan L, Smith V, Trouard T. A functional imaging study of cooperation in two-person reciprocal exchange. Proc Natl Acad Sci U S A 2001; 98: 11832-5.

McClelland JL, Rogers TT. The parallel distributed processing approach to semantic cognition. Nat Rev Neurosci 2003; 4: 310-22.

Miller EK, Cohen JD. An integrative theory of prefrontal cortex function. Annu Rev Neurosci 2001; 24: 167-202.

Mitchell JP. Activity in right temporo-parietal junction is not selective for theory-of-mind. Cereb Cortex 2008; 18: 262-71.

Mitchell JP, Macrae CN, Banaji MR. Dissociable medial prefrontal contributions to judgments of similar and dissimilar others. Neuron 2006; 50: 655-63.

Moll J, de Oliveira-Souza R, Eslinger PJ, Bramati IE, Mourao-Miranda J, Andreiuolo PA, et al. The neural correlates of moral sensitivity: a functional magnetic resonance imaging investigation of basic and moral emotions. J Neurosci 2002; 22: 2730-6.

Moll J, Krueger F, Zahn R, Pardini M, de Oliveira-Souza R, Grafman J. Human fronto–mesolimbic networks guide decisions about charitable donation. Proc Natl Acad Sci U S A 2006; 103: 15623-8.

Moll J, Zahn R, de Oliveira-Souza R, Krueger F, Grafman J. Opinion: the neural basis of human moral cognition. Nat Rev Neurosci 2005; 6: 799-809.

Nelson K, Gruendel J. Generalized event represenations: Basic building blocks of cognitive development. In: Lamb ME and Brown AL, editors. Advances in developmental psychology. Vol 1. Hillsdale, NJ: Erlbaum, 1981: 131-158.

Northoff G, Bermpohl F. Cortical midline structures and the self. Trends Cogn Sci 2004; 8: 102-7.

Northoff G, Heinzel A, de Greck M, Bermpohl F, Dobrowolny H, Panksepp J. Self-referential processing in our brain: a meta-analysis of imaging studies on the self. Neuroimage 2006; 31: 440-57.

Numan R, editor. The behavioral neuroscience of the septal region. New York: Springer, 2000.

O'Doherty JP, Buchanan TW, Seymour B, Dolan RJ. Predictive neural coding of reward preference involves dissociable responses in human ventral midbrain and ventral striatum. Neuron 2006; 49: 157-66.

Ongur D, Ferry AT, Price JL. Architectonic subdivision of the human orbital and medial prefrontal cortex. J Comp Neurol 2003; 460: 425-49.

Pandya DN, Yeterian EH. In: Damasio AR, Damasio H and Christen Y, editors. Neurobiology of Decision Making. Berlin: Springer, 1996: 13-46.

Partiot A, Grafman J, Sadato N, Flitman S, Wild K. Brain activation during script event processing. Neuroreport 1996; 7: 761-6.

Paus T, Zijdenbos A, Worsley K, Collins DL, Blumenthal J, Giedd JN, et al. Structural maturation of neural pathways in children and adolescents: in vivo study. Science 1999; 283: 1908-11.

Pietrini P, Guazzelli M, Basso G, Jaffe K, Grafman J. Neural correlates of imaginal aggressive behavior assessed by positron emission tomography in healthy subjects. Am J Psychiatry 2000; 157: 1772-81.

Porrino LJ, Crane AM, Goldman-Rakic PS. Direct and indirect pathways from the amygdala to the frontal lobe in rhesus monkeys. J Comp Neurol 1981; 198: 121-36.

Price JL. Prefrontal cortical networks related to visceral function and mood. Ann N Y Acad Sci 1999; 877: 383-96.

Ramnani N, Owen AM. Anterior prefrontal cortex: insights into function from anatomy and neuroimaging. Nat Rev Neurosci 2004; 5: 184-94.

Rilling J, Gutman D, Zeh T, Pagnoni G, Berns G, Kilts C. A neural basis for social cooperation. Neuron 2002; 35: 395-405.

Rilling JK, Insel TR. The primate neocortex in comparative perspective using magnetic resonance imaging. J Hum Evol 1999; 37: 191-223.

Rilling JK, Sanfey AG, Aronson JA, Nystrom LE, Cohen JD. The neural correlates of theory of mind within interpersonal interactions. Neuroimage 2004; 22: 1694-703.

Rolls ET. The brain and emotion. Oxford: Oxford University Press, 1999.

Ruby P, Sirigu A, Decety J. Distinct areas in parietal cortex involved in long-term and short-term action planning: a PET investigation. Cortex 2002; 38: 321-39.

Rueckert L, Grafman J. Sustained attention deficits in patients with lesions of posterior cortex. Neuropsychologia 1998; 36: 653-60.

Schank R, Abelson P. Scripts, plans, goals and understanding. Hillsdale, NJ: Erlbaum, 1977.

Schore AN. Affect dysregulation and disorder of the self. New York, NY: W. W. Norton, 2003.

Schultz W, Dayan P, Montague PR. A neural substrate of prediction and reward. Science 1997; 275: 1593-9.

Schultz W, Tremblay L, Hollerman JR. Reward prediction in primate basal ganglia and frontal cortex. Neuropharmacology 1998; 37: 421-9.

Semendeferi K, Armstrong E, Schleicher A, Zilles K, van Hoesen GW. Prefrontal cortex in humans and apes: a comparative study of area 10. Am J Phys Anthropol 2001; 114: 224-241.

Semendeferi K, Lu A, Schenker N, Damasio H. Humans and great apes share a large frontal cortex. Nat Neurosci 2002; 5: 272-276.

Shallice T. Specific impairments of planning. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 1982; 298: 199-209.

Shallice T, Burgess PW. Deficits in strategy application following frontal lobe damage in man. Brain 1991; 114 (Pt 2): 727-41.

Singer T, Kiebel SJ, Winston JS, Dolan RJ, Frith CD. Brain responses to the acquired moral status of faces. Neuron 2004; 41: 653-62.

Sirigu A, Zalla T, Pillon B, Grafman J, Agid Y, Dubois B. Encoding of sequence and boundaries of scripts following prefrontal lesions. Cortex 1996; 32: 297-310.

Sirigu A, Zalla T, Pillon B, Grafman J, Dubois B, Agid Y. Planning and script analysis following prefrontal lobe lesions. In: Grafman J, Holyoak KJ and Boller F, editors. Structure and functions of the human prefrontal cortex. New York: New York Academy of Sciences, 1995: 277-288.

Soloff PH, Meltzer CC, Greer PJ, Constantine D, Kelly TM. A fenfluramine-activated FDG-PET study of borderline personality disorder. Biol Psychiatry 2000; 47: 540-7.

Sowell ER, Thompson PM, Holmes CJ, Jernigan TL, Toga AW. In vivo evidence for post-adolescent brain maturation in frontal and striatal regions. Nat Neurosci 1999; 2: 859-61.

Strenziok M, Krueger F, Heinecke A, Lenroot RK, Knutson KM, van der Meer E, et al. Developmental effects of aggressive behavior in male adolescents assessed with structural and functional brain imaging. Soc Cogn Affect Neurosci 2009.

Stuss DT, Benson DF. Neuropsychological studies of the frontal lobes. Psychol. Bull. 1984; 95: 3-28.

Stuss DT, Benson DF. The frontal lobes. New York: Raven Press, 1986.

Stuss DT, Gallup GG, Jr., Alexander MP. The frontal lobes are necessary for 'theory of mind'. Brain 2001; 124: 279-86.

Tanaka SC, Doya K, Okada G, Ueda K, Okamoto Y, Yamawaki S. Prediction of immediate and future rewards differentially recruits cortico-basal ganglia loops. Nat Neurosci 2004; 7: 887-93.

Taylor SE, Crocker J. Schematic bases of social information processing. In: Higgens ET, Herman CP and Zanna MP, editors. Social cognition: The Ontario symposium. Vol 1. Hillsdale, NJ: Erlbaum, 1981: 89-134.

Tremblay L, Schultz W. Reward-related neuronal activity during go-nogo task performance in primate orbitofrontal cortex. J Neurophysiol 2000; 83: 1864-76.

Van Overwalle F. Social cognition and the brain: A meta-analysis. Hum Brain Mapp 2008.

Wood JN, Grafman J. Human prefrontal cortex: processing and representational perspectives. Nat Rev Neurosci 2003; 4: 139-47.

Wood JN, Knutson KM, Grafman J. Psychological structure and neural correlates of event knowledge. Cereb Cortex 2005; 15: 1155-61.

Young LJ, Wang Z. The neurobiology of pair bonding. Nat Neurosci 2004; 7: 1048-54.

Zacks JM, Braver TS, Sheridan MA, Donaldson DI, Snyder AZ, Ollinger JM, et al. Human brain activity time-locked to perceptual event boundaries. Nat Neurosci 2001; 4: 651-5.

Zacks JM, Tversky B. Event structure in perception and conception. Psychol Bull 2001; 127: 3-21.

Zahn R, Moll J, Krueger F, Huey ED, Garrido G, Grafman J. Social concepts are represented in the superior anterior temporal cortex. Proc Natl Acad Sci U S A 2007; 104: 6430-5.

Zamboni G, Gozzi M, Krueger F, Duhamel JR, Sirigu A, Grafman J. Individualism, conservatism, and radicalism as criteria for processing political beliefs: A parametric fMRI study. Soc Neurosci 2009: 1-17.

3. Statements of Authorship and Originality

This habilitation synopsis is entirely my own work. To the best of my knowledge and belief, it does not contain any material previously published or written by another person, except where due reference is made in this synopsis itself. Neither the habilitation synopsis, nor any section thereof, has been previously submitted towards a degree or diploma in any university or other higher education institution.

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Place and date signed Signature

4. Submitted Articles

SOCIAL EVENT KNOWLEDGE AND EVENT SCHEMATA

[1] **Krueger, F.,** Moll, J., Zahn, R., Heinecke, A., & Grafman, J. (2007). Event frequency modulates the processing of daily life activities in human medial prefrontal cortex. *Cereb Cortex, 17*(10), 2346-2353.

[2] **Krueger, F.**, Spampinato, M. V., Barbey, A., Huey, E., & Morland, T. & Grafman, J. (2009). The role of the frontopolar cortex in mediating action complexity: A parametric fMRI study. *Neuroreport,* 20: 1093-1097.

[3] Strenziok, M.[*], **Krueger, F.**[*], Heinecke, A., Lenroot, R. K., Knutson, K. M., van der Meer, E., & Grafman, J. (2009). Developmental effects of aggressive behavior in male adolescents assessed with structural and functional brain imaging. *Social Cognitive and Affective Neuroscience.* [10.1093/ scan/ nsp036].
[*]Authors contributed equally to this work.

SOCIAL EVENT KNOWLEDGE AND PERSON SCHEMATA

[4] **Krueger, F.**, McCabe, K., Moll, J., Kriegeskorte, N., Zahn, R., Strenziok, M., Heinecke, A., & Grafman, J. (2007). Neural correlates of trust. *Proc Natl Acad Sci U S A, 104*(50), 20084-20089.

[5] **Krueger, F.**, Grafman, J., & McCabe, K. (2008). Neural correlates of economic game playing. *Philos Trans R Soc Lond B Biol Sci, 363*(1511): 3859-3874.

[6] Zahn, R., Moll, J., **Krueger, F.**, Huey, E. D., Garrido, G., & Grafman, J. (2007). Social concepts are represented in the superior anterior temporal cortex. *Proc Natl Acad Sci U S A, 104*(15), 6430-6435.

SOCIAL EVENT KNOWLEDGE AND SELF SCHEMATA

[7] Zamboni, G., Gozzi M., **Krueger, F.**, Duhamel, J.R., Sirigu, A., & Grafman, J. (2009). Individualism, conservatism, and radicalism as criteria for processing political beliefs: a parametric fMRI study. *Social Neuroscience*: 1-17.

[8] Moll, J., **Krueger**, F., Zahn, R., Pardini, M., de Oliveira-Souza, R., & Grafman, J. (2006). Human fronto–mesolimbic networks guide decisions about charitable donation. *Proc Natl Acad Sci U S A, 103*(42), 15623-15628.

[9] **Krueger, F.**, Barbey A., McCabe, K., Strenziok, M., Zamboni, G., Solomon, J., Raymont, V., & Grafman, J. (2009). The neural bases of key competencies of emotional intelligence. *Proc Natl Acad Sci U S A*, *106*(52): 22468-22491.